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COMPARATIVE MORPHOLOGY OF SOME LEGUMINOSAE

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 190

JOHN N. MARTIN

(WITH PLATES VIII–XI)

This investigation covers the development of the embryo sac, embryo, and endosperm of *Trifolium pratense*, *T. hybridum*, *T. repens*, *Medicago sativa*, and *Vicia americana*. The work was done at the University of Chicago and Iowa State College. I wish to express my thanks to Professor COULTER and Professor CHAMBERLAIN who supervised the work, and to Professor PAMMEL at Iowa State College for valuable suggestions.

Historical

In 1839 and 1842 SCHLEIDEN and VOGEL (8) described the floral development and the endosperm of the Leguminosae. They investigated the endosperm of more than 50 species well distributed through the group. They found only a little endosperm remaining in *Trifolium* and *Medicago*, and none in *Vicia*. In 1855 TULASNE (13) described the proembryo of *Lathyrus Aphaca;* it produced a long filamentous suspensor and a distinct terminal embryo. HOFMEISTER (5) in 1858 described the embryo sac and proembryo of some species of *Lotus*, *Tetragonolobus*, *Trifolium*, *Lupinus*, and *Lathyrus;* he found a short massive proembryo in *Trifolium*. In 1880 STRASBURGER (10) described a proembryo developing a long suspensor in several species of *Lupinus* and in *Orobus vernus;* the cells of the suspensor are multinucleate and often separate. In the same year HEGELMAIER (4) reported the results of his investigations of the embryo sac, proembryo, and endosperm in four species of *Lupinus*. He found that the cells of the filamentous suspensor are multinucleate and that ephemeral cell plates appear during the division of the endosperm nuclei. In 1881 GUIGNARD'S (3) work appeared, covering about 40 species of the Leguminosae,

well distributed through the family. At that time the homology between microsporangium and megasporangium had not been established, and the terms "apical" and "subapical" were used to designate the primary parietal and sporogenous cells. His account shows that a one-celled archesporium prevails through the group. The archesporial cell always cuts off one parietal cell, which may remain undivided or produce a tissue varying in amount. The megaspore mother cell may produce the embryo sac directly, or form an axial row of 2, 3, or 4 cells, of which the innermost or one next to it may function. The embryo sac is always 8-celled and the antipodals are ephemeral. The fusion of the polar nuclei may occur in the center of the sac, against the inner wall, or in contact with the egg apparatus. The first division of the egg is transverse. The following divisions may result in a massive proembryo with no distinct line between the massive suspensor and embryo, or in a proembryo with a slender suspensor and a sharply defined terminal embryo. In 1907 SAXTON (7) described the embryo sac of *Cassia tomentosa*, and found one *deeply* buried megaspore mother cell. The third megaspore out of the longitudinal row of 4 functions; the polars fuse early; and the antipodals are persistent and form an absorptive tissue which fills the tubular projection in the chalazal region.

In 1912 COMPTON (1) described the seedling structure of 201 species of Leguminosae, ranging through all the regions of the vast family. He found the seedling epigeal in *Trifolium* and *Medicago*, but hypogeal in *Vicia*.

Material

Several fixing agents were tried, but chromo-acetic acid gave best results; one-half of 1 per cent strength was most satisfactory. The heads of *Trifolium* were split and entire halves run through and sectioned. Since the head is a compact raceme, this method enables one to trace the development of the embryo sac more readily, and proved to be of valuable assistance in determining the sterility of ovules. Separate flowers of *Medicago* and *Vicia* were used. The sections were stained with safranin and gentian violet.

Trifolium pratense

A more thorough study was made of this species because of its economic importance, and it was hoped that a better knowledge of its morphology would aid in controlling seed production. The discussion of *Trifolium pratense* will be somewhat detailed, and will form a basis for a comparative treatment of the other 4 species.

The ovary develops invariably 2 campylotropous ovules which are attached to a cushion-like placenta (fig. 1). The outer integument, which is barely a distinct ridge when the inner appears, soon passes the inner and forms a heavy rim about the micropyle (figs. 8, 10). The outer integument, which varies from 2 to 4 rows of cells in thickness at fertilization, except at the micropyle, thickens by periclinal divisions to many rows after fertilization, and the outer row of cells forms the peculiarly thickened and cutinized layer of the testa. The inner integument usually remains two layers in thickness until destroyed by the embryo sac. Sometimes three layers are seen in its basal region (fig. 10).

The nucellus is hemispherical at the time the archesporium can be identified, but elongates rapidly and is quite slender at the time the embryo sac is mature (fig. 12). There are usually 3 subepidermal rows (fig. 3), but often 3–6 rows are found at the base of the nucellus (fig. 12).

EMBRYO SAC.—From 1 to 4 archesporial cells were observed, and more than half of the ovules showed more than one archesporial cell. In fig. 3 there are 4 archesporial cells in a longitudinal row. In fig. 4 there are 4, but 3 are hypodermal and the other is more deeply placed. In either case, it is probable that the 4 archesporial cells have come from the division of a hypodermal cell at an early stage in the development of the nucellus. It is also probable that the cells deeper than the hypodermal layer may become sporogenous. One parietal cell is cut off (fig. 2), which usually divides transversely to form a longitudinal row of 2 or 3 cells (fig. 8), or one transverse and one longitudinal division may occur (fig. 6). No division (fig. 7) or only a longitudinal division has been observed. In fig. 5 two of the three megaspore mother cells have reached the synapsis stage, but more than one row of megaspores was not found.

So far as observed, a longitudinal row of 4 megaspores is always formed and the lower one functions (figs. 7, 8).

No chromosome counts were made, but the number is small and probably the same as in *Trifolium repens*, where it is about 12. The functioning megaspore rapidly destroys the surrounding tissue. The encroachment is at first most rapid at the chalazal end and results in a tubular sac (figs. 9, 10). As the megaspore enlarges, the tip of the nucellus thickens and with the surrounding portion of the inner integument becomes packed with starch (fig. 10). The megaspore divides in the direction of the long axis of the sac and the daughter nuclei pass to opposite poles (fig. 9). The following divisions may be parallel or transverse to the long axis of the sac (figs. 10–12). The longitudinal divisions are no doubt associated with the narrowness of the sac and occur most often in the antipodal end. As the embryo sac matures, it destroys the micropylar end of the nucellus and becomes much larger in this region (fig. 11). When the sac is mature, only the basal portion of the nucellus remains and the embryo sac lies against the inner integument (fig. 13). Sometimes the nucellus is more persistent, as shown in fig. 12.

The polar nuclei usually meet on the median line of the sac close to the egg apparatus (fig. 12), but occasionally they lie against the inner wall of the sac. Fusion awaits fertilization, but was found to occur if fertilization was prevented. Fig. 14 shows the fusion of the two polars before fertilization. In this case pollination was prevented and the ovaries were killed soon after the flowers began wilting.

The synergids often show a distinct filiform apparatus (fig. 14), which becomes more prominent if fertilization is prevented. The antipodals are ephemeral and no trace of them is left at the time of fertilization.

FERTILIZATION.—The fusion of the sex nuclei was not seen, although many flowers were pollinated and killed at various periods after pollination. The time between pollination and fertilization varies. Flowers pollinated during the high temperature of July and killed 18 hours after pollination showed pollen tubes entering, egg in first division, and 3-celled embryos. In October, when the

temperature was much lower, the time of fertilization ranged from 35 to 50 hours. This difference, no doubt, is partly due to a difference in growth conditions, and partly to delayed germination of the pollen. During the cooler weather pollen placed on the stigma at 3:00 P.M. was found dormant at 9:00 A.M. on the following day. This delayed germination will cause a marked difference in the time of fertilization. The pollen tube enters around the wall or in the region of a synergid (fig. 15); its behavior with reference to the synergid was not determined.

EMBRYO.—The first divisions of the egg are transverse (fig. 17), and result in a filament of three cells (fig. 18). By vertical walls in two planes this filament is divided into tiers of 4 cells each (fig. 19). The basal tier and a part of the second tier remain less active, but later form a massive suspensor (figs. 20, 21). No distinct line between embryo and suspensor was made out. In fig. 20 the dermatogen is being differentiated, which occurs later than the octant stage.

ENDOSPERM.—The division of the endosperm nucleus usually precedes that of the egg (fig. 15), but occasionally follows it (fig. 16). In fig. 17 the fertilized egg has completed its first division, and 5 endosperm nuclei were counted. The endosperm masses about the embryo and from this mass it extends around the wall of the sac. Its later development is centripetal. Only the first division of the endosperm nucleus was seen in the many ovules studied. This fact indicates that the divisions in the endosperm nuclei are simultaneous, but this feature was not determined.

STERILITY.—The sterility of ovules is a prominent feature in *Trifolium pratense*. In the sterile ovules all the cells of the nucellus remain vegetative and hence no embryo sacs are found. All the flowers of a plant frequently develop sterile ovules only. This seems to be related to moisture conditions, but more work is necessary before a definite conclusion can be drawn as to its cause. Plants grown in the greenhouse and well watered gave 100 per cent sterile ovules. First crop heads collected from the field during wet weather showed nearly 100 per cent sterility, while first crop heads collected after two weeks of dry weather showed a large percentage of fertile ovules. But even during dry weather

there is considerable variation among plants, some producing nearly all fertile ovules, and others a large percentage of sterile ones. There is a marked tendency toward sterility, which seems to be favored by moisture. This tendency, no doubt, always lowers the percentage of seed production, and in some cases reduces it almost to zero. The fact that this tendency varies among plants under similar conditions suggests that it may be partly eliminated by selection. A sterile ovule is shown in fig. 22. The flower was open and the embryo sac should have been ready for fertilization. Sterile ovules can be identified only in later stages. The cells of the subepidermal rows are usually larger and less dense in content, but it is safe to pass judgment on the earlier stages only when all the later stages of the head are sterile. No mother cells in synapsis were found in the sterile ovules, so sterility seems to be determined before this stage is reached.

PARTHENOGENESIS.—*Trifolium pratense* has been reported parthenogenetic. Flowers were run under cover and killed at various times after wilting. An examination of more than 500 ovaries showed no embryos. The ovule enlarges very rapidly for several days after the embryo sac is ready for fertilization and then begins to break down.

Trifolium hybridum

This species is so similar to *Trifolium pratense* that a few features only deserve mention. The number of ovules in an ovary is variable, ranging from 3 to 8. Fig. 23 shows the lower megaspore germinating before the others are destroyed. The embryo sac has a large central vacuole and the cytoplasm is almost entirely limited to a thin peripheral layer (fig. 24). The embryo sac becomes more curved than that of *Trifolium pratense* (fig. 27). The polars fuse in a parietal position (fig. 24). The proembryo is more slender and there is a more definite line between embryo and suspensor in the later stages (fig. 25). Fig. 25 also shows the faint walls that sometimes occur in the early development of the endosperm. Fig. 26 shows the suspensor on the hypocotyl of the embryo. The tendency toward sterility is not so pronounced in this species as it is in *Trifolium pratense*.

Trifolium repens

This species agrees very closely with *Trifolium hybridum*. Fig. 28 shows the reduction division of the mother cell; 11 chromosomes are shown, but various counts gave 11 and 12. The number is small, about 12. In fig. 29 one megaspore mother cell has produced 4 megaspores, while the other one has enlarged but has made no division. The third megaspore often functions (fig. 30). The embryo does not differ from that of *Trifolium hybridum*. The endosperm masses about the embryo in its early development, but no walls occur. Not much sterilization was observed.

Medicago sativa

In *Medicago sativa* the number of ovules in an ovary varies considerably, ranging between 12 and 18. The nucellus is more massive than that of *Trifolium*. The number of subepidermal rows ranges from 5 to 7 (figs. 31, 34). The outer integument precedes the inner as in *Trifolium*. The number of archesporial cells ranges from 1 to 6, and more than one usually occurs (fig. 31). One parietal cell is nearly always cut off, but occasionally megaspore mother cells may be found with no parietal cells (fig. 32). The parietal cell usually makes only one division, which is transverse (figs. 32, 33), but at times the transverse division is followed by one or more longitudinal ones (fig. 34). Prominent cell plates accompany the formation of the megaspores (figs. 33, 34). From 2 to 4 rows of megaspores may occur in the same nucellus (fig. 34) and often more than one megaspore starts to form an embryo sac (fig. 35), but not more than one mature sac was found. The embryo sac destroys the surrounding nucellar tissue more uniformly and does not become so tubular as in *Trifolium* (figs. 36, 37). The large central vacuole which appears during the formation of the 8 nuclei (fig. 36) disappears later, and the cytoplasm becomes compact and filled with starch (fig. 37). The 8 nuclei of the embryo sac are arranged in two groups of 4 each, separated by the large vacuole (fig. 36), and when the embryo sac is mature, 3 nuclei of each group are definitely set off at the poles in separate masses of cytoplasm, while the 2 polar nuclei occupy the median mass of cytoplasm (fig. 37). The polars meet near the middle of the sac

(fig. 37) and then move to a position near the egg apparatus (fig. 38), where they fuse late, probably not until fertilization. Three antipodals are usually formed (fig. 36), but sometimes only one division occurs in the antipodal end, which results in only one antipodal cell (fig. 37). The antipodals disappear before the embryo sac is mature (fig. 38).

EMBRYO.—The egg forms a filament of 5 cells, the terminal one of which produces the embryo, while the other 4 constitute the suspensor (figs. 39, 40). The basal cell of the suspensor is quite long. All the cells have thin, granular cytoplasm and are usually multinucleate. The suspensor is still seen on the advanced embryo (fig. 41). Fig. 40 shows the embryo with dermatogen already differentiated.

ENDOSPERM.—The endosperm takes the parietal arrangement with the earlier development in the micropylar end, but does not mass about the embryo as in the clovers (fig. 40). No sterility was observed in *Medicago sativa*, but all material used, so far, was collected during rather dry periods, and further investigation is necessary to determine the effect of moisture upon its fertility.

Vicia americana

The number of ovules in *Vicia americana* has about the same range as in *Medicago sativa*. The nucellus is smaller, usually having 3 or 4 subepidermal rows. Periclinal divisions are rapid in the early stage of the nucellus, which give it a slender form. The outer integument, as in *Trifolium* and *Medicago*, precedes the inner. Fig. 42 shows 5 archesporial cells, all of which are probably not of hypodermal origin. The development of parietal tissue is variable, as shown by figs. 43–45. A row of 4 megaspores is formed (fig. 44) and the lower functions (fig. 45).

The embryo sac resembles that of *Medicago sativa* in formation, shape, and in the destruction of nucellar tissue. The antipodals are ephemeral as in the other species (figs. 46, 47), but the position of the polars is near the inner wall in the middle of the sac (fig. 47). It resembles the clover in having much starch in the inner integument and little in the sac.

EMBRYO.—The proembryo consists of a filament of three cells, of which the terminal forms the embryo, while the other two form a long suspensor of two tiers of two cells each. The cells of the suspensor have very little cytoplasm and are multinucleate (figs. 48–51).

ENDOSPERM.—The endosperm nucleus and egg divide at about the same time. The endosperm nuclei divide rapidly and simultaneously. The endosperm is parietally placed and does not mass about the proembryo in the early stages of its development (figs. 52, 53). Some sterile ovules were found, but the tendency toward sterility is not so pronounced as in the clovers.

Discussion

GUIGNARD'S account of *Trifolium* (**3**, pp. 119, 120) is limited to the development of the embryo. The fertilized egg produces a filament of 3 cells, the terminal of which develops the embryo. The other 2 cells produce a short, several-celled suspensor. In the later stages the line of separation between embryo and suspensor is indistinct. The dermatogen is differentiated in the octant stage. In the three species of *Trifolium* investigated by the writer, the suspensor is more massive and the dermatogen is differentiated later than the octant stage.

In *Medicago arborea* GUIGNARD (**3**, pp. 119, 120, *figs. 192–194*) reports a one-celled archesporium and two superimposed parietal cells. The megaspore mother cell functions directly to produce the embryo sac. The proembryo produces a long, filamentous suspensor which is distinct from the terminal embryo. The dermatogen is differentiated in the octant stage. In *Medicago sativa* there is usually a multicellular archesporium, production of megaspores, and more parietal tissue, but in other features it is similar to *Medicago arborea*. In *Vicia sepium*, GUIGNARD (**3**, p. 53, *figs. 66–70*) found one parietal cell which occasionally makes one transverse division. The single megaspore mother cell produces a longitudinal row of 3 cells, the lower 2 being megaspores, or a longitudinal row of 4 megaspores; in each case the lowest megaspore functions. The proembryo produces a long suspensor which consists of two rows of cells and is distinct from the embryo. In *Vicia americana* a

multicellular archesporium usually occurs, and so far as observed a longitudinal row of 4 megaspores is always formed.

GUIGNARD gives no account of a multicellular archesporium in any of the species which he studied, but the early stages of the ovules were examined without sectioning, and it is probable that present methods would give different results. He found parietal tissue in all species studied, but the greatest amount in the Mimosoideae and Caesalpinioideae.

The following records show that a multicellular archesporium occurs in other families of the Rosales. Miss PACE (**6**) found a multicellular archesporium in *Parnassia* and *Saxifraga*. WEBB (**14**) reported the same type in *Astilbe*. SHOEMAKER (**9**) found several archesporial cells in *Hamamelis;* and COULTER and CHAMBERLAIN (**2**, pp. 58, 59) in a summary of the literature show that a multicellular archesporium prevails among the Rosaceae.

The filiform apparatus in *Trifolium pratense* differs from that described by PACE in *Parnassia* and *Saxifraga* and by STRASBURGER in *Polygonum* (**11**) and *Santalum* (**12**), in that no notch appears.

GUIGNARD (**3**, p. 142) states that the polar nuclei fuse before fertilization except in the subfamily Vicieae, and that the fusion nucleus rests on the median line of the sac in the Mimosoideae and Caesalpinioideae, and against the inner side of the sac in the Papilionoideae. In the five species treated in this paper, the fusion of the polar nuclei was found to await fertilization, and their position is median in *Medicago sativa*, but may be either median or parietal in the species of *Trifolium*, and always parietal in *Vicia americana*.

GUIGNARD (**3**, p. 141) found the antipodal cells persisting till fertilization in the Mimosoideae and Caesalpinioideae, but disappearing earlier in the Papilionoideae. SAXTON (**7**) found the antipodals persistent and functioning as haustoria in *Cassia tomentosa*.

Summary

Features common to the five species are as follows: (1) campylotropous ovules; (2) two integuments, the outer preceding the inner; (3) a multicellular archesporium; (4) one parietal cell cut off which gives rise to more or less parietal tissue; (5) the production of a row of 4 megaspores; (6) the rapid destruction of

nucellar tissue which brings the embryo sac in contact with the inner integument; (7) antipodals ephemeral.

Contrasting features are as follows: (1) the number of ovules is always 2 in *Trifolium pratense*, but more than 2 and various in the other species; (2) the third megaspore sometimes functions in *T. repens;* (3) in *Trifolium* the embryo sac rapidly destroys the antipodal end of the nucellus and thus forms a long tubular sac; (4) in *Trifolium* the embryo sac remains very vacuolate, while in *Vicia* and *Medicago* the sac fills with cytoplasm; (5) polars meet on median line or on inner side of sac in *Trifolium*, but rest near the egg apparatus; in *Medicago* the polars meet near the center of the sac and rest near the egg apparatus; while in *Vicia* they meet on the inner side of the sac and remain some distance from the egg apparatus; (6) in *Trifolium* and *Vicia*, the starch appears in the micropylar end of the nucellus and in the inner integument, while the starch fills the sac in *Medicago;* (7) in *Trifolium* the proembryo is short and massive and no definite line between suspensor and embryo was made out; more evidence of the separate parts was seen in the more slender proembryos of *T. hybridum* and *T. repens;* (8) definite suspensors with multinucleate cells appear in *Medicago sativa* and *Vicia americana;* in the former species the suspensor is filamentous, but composed of two superimposed pairs of cells in the latter species; (9) sterilization is most marked in *T. pratense*.

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EXPLANATION OF PLATES VIII–XI

Trifolium pratense

FIG. 1.—Young ovary showing the two ovules and placenta; ×330.

FIG. 2.—Young nucellus showing one sporogenous and one parietal cell; ×1560.

FIG. 3.—Young nucellus with a row of 4 archesporial cells; both integuments are prominent; ×1500.

FIG. 4.—Young nucellus with 4 archesporial cells; inner integument is just beginning to show; ×1560.

FIG. 5.—Cross-section of nucellus with 3 megaspores, 2 of which are in synapsis; ×1500.

FIG. 6.—Young nucellus with one mother cell in synapsis; the integuments are well advanced; ×1200.

FIG. 7.—Nucellus with a row of 4 megaspores; two large dense cells lie in line below the megaspores; parietal cell has not divided; ×1200.

FIG. 8.—Four megaspores with lower one functioning; ×1500.

FIG. 9.—A binucleate embryo sac eating its way into the chalazal end of the nucellus; ×1560.

FIG. 10.—A 4-nucleate embryo sac; the divisions at each end have been in the direction of the long axis of the sac; integuments well advanced and outer is thickened at micropylar end; the ends of the nucellus and the inner integument are filled with starch; ×880.

FIG. 11.—An 8-nucleate sac, with linear arrangement at antipodal end; micropylar end of nucellus being destroyed; embryo sac quite vacuolate; ×920.

FIG. 12.—Polars in contact near the egg apparatus; nucellus more persistent; ×1200.

FIG. 13.—Embryo sac mature and in contact with inner integument; ×920.

FIG. 14.—Egg apparatus with synergids showing filiform apparatus; the nucleoli of the polars are fusing; ×1560.

FIG. 15.—Pollen tube in region of synergid, and egg in division; endosperm cell has made one division; ×920.

FIG. 16.—A 2-celled proembryo, while the endosperm cell is in first division; ×920.

FIG. 17.—A 2-celled proembryo; 5 endosperm nuclei were counted; ×920.

FIG. 18.—A 3-celled proembryo; ×920.

FIG. 19.—Proembryo has divided by vertical walls; ×750.

FIG. 20.—Dermatogen is cut off; ×750.

FIG. 21.—The massive proembryo with no line of separation between embryo and suspensor; ×540.

FIG. 22.—Median longitudinal section of a sterile ovule; embryo sac replaced by vegetative cells; ×1200.

Trifolium hybridum

FIG. 23.—Early germination of lower megaspore; ×1500.

FIG. 24.—An 8-nucleate embryo sac; cytoplasm of the sac forms a marginal layer around the large vacuole; polars in contact on inner side of sac; ×910.

FIG. 25.—Proembryo with cotyledons appearing; the stalk is composed of large cells, and there is an apparent line of separation between suspensor and embryo at this stage; ×540.

FIG. 26.—Remains of suspensor on the hypocotyl of the embryo; ×530.

FIG. 27.—Ovule showing the long, curved embryo sac, and proembryo in early stage; ×360.

Trifolium repens

FIG. 28.—Reduction division of mother cell; outer integument well developed; ×1500.

FIG. 29.—One row of megaspores and one enlarged mother cell; ×1500.

FIG. 30.—Third megaspore functioning; ×1200.

Medicago sativa

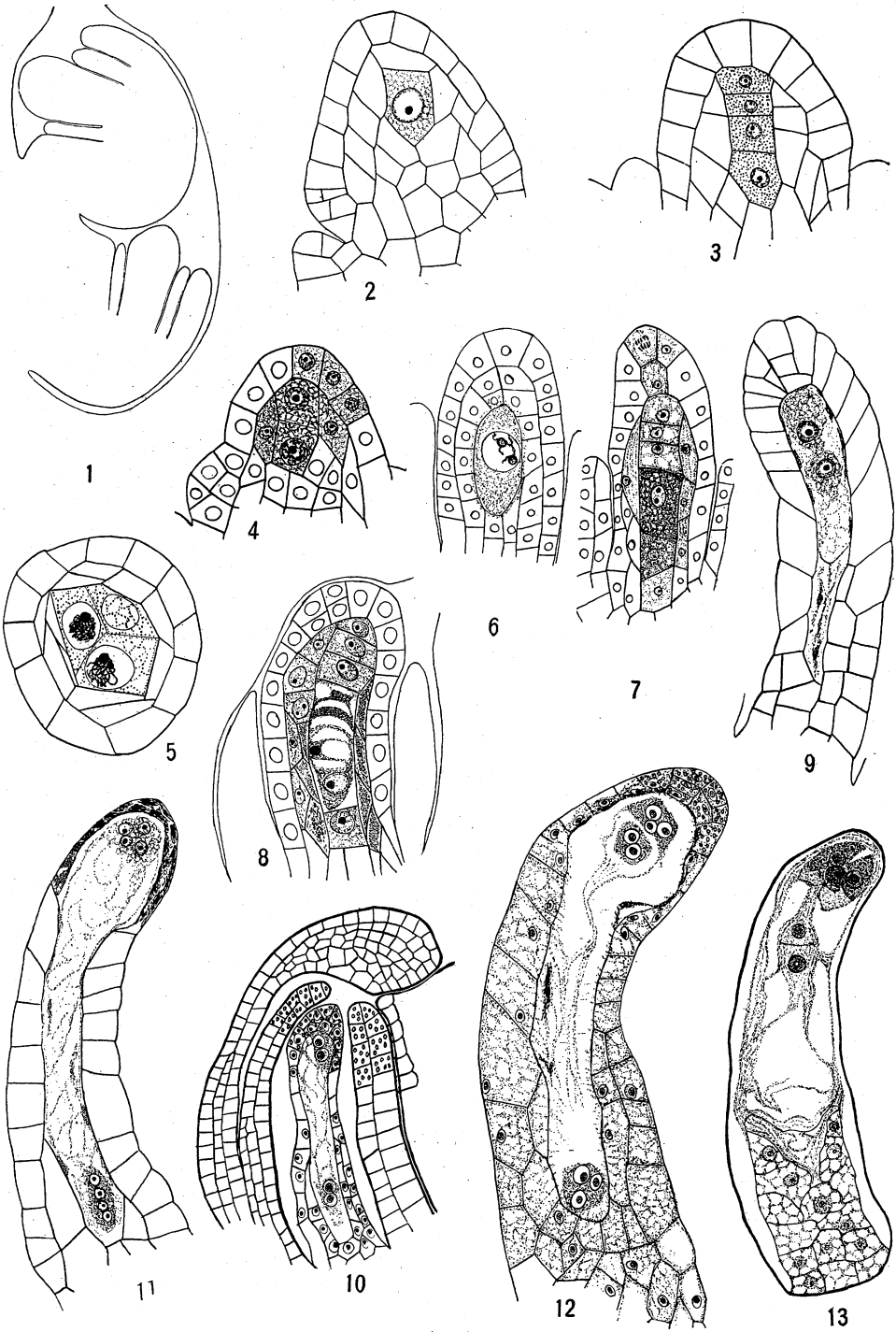
FIG. 31.—Young nucellus with 3 sporogenous cells, each capped by one parietal cell; ×1500.

FIG. 32.—Three mother cells in synapsis; two have no parietal cells; ×1500.

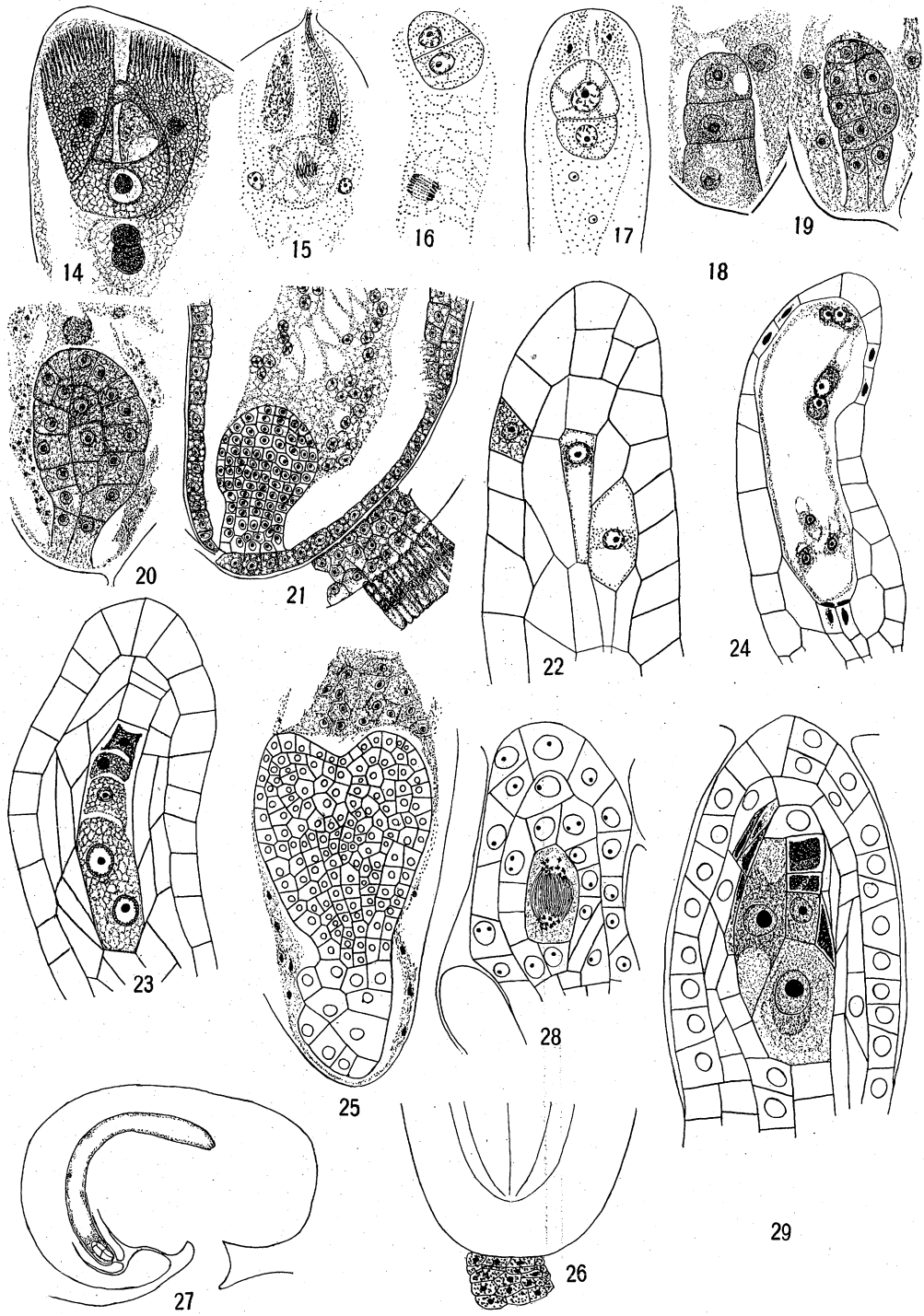
FIG. 33.—Mother cell in reduction division; parietal cell has divided transversely; ×1500.

FIG. 34.—Two rows of megaspores; ×1500.

FIG. 35.—Two embryo sacs; one is binucleate; ×1500.



MARTIN on LEGUMINOSAE



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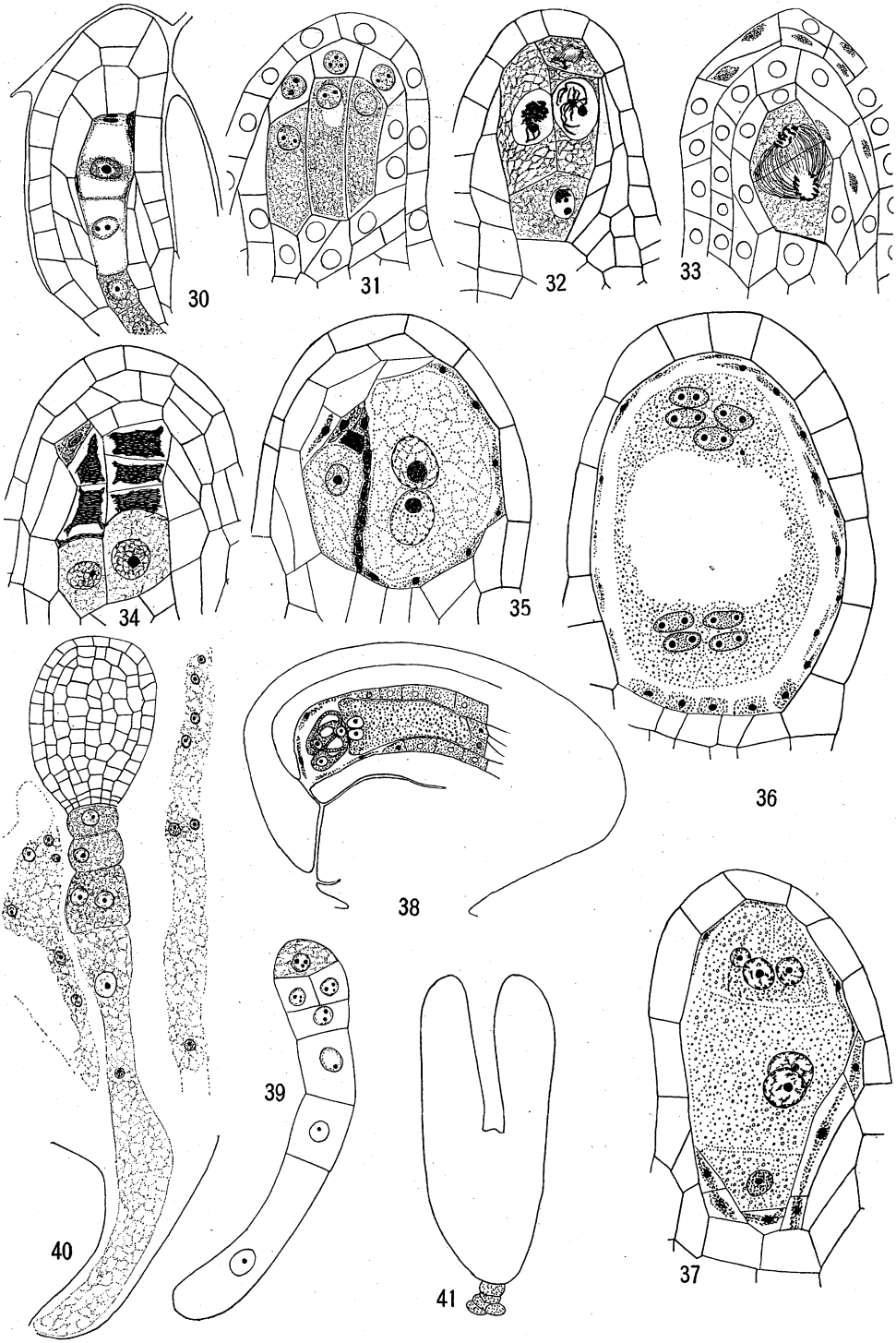

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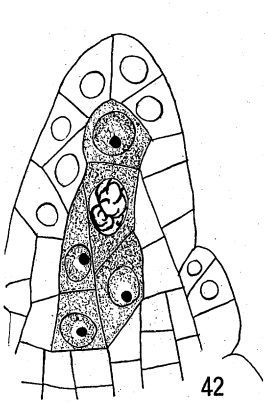
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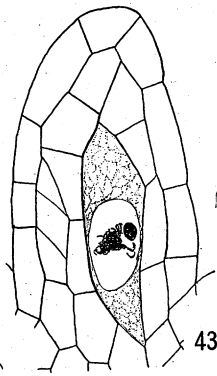
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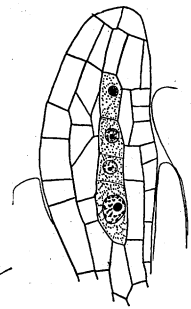
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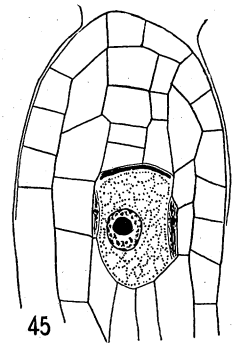
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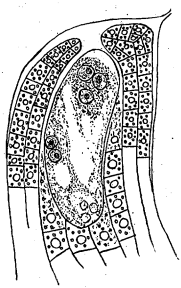
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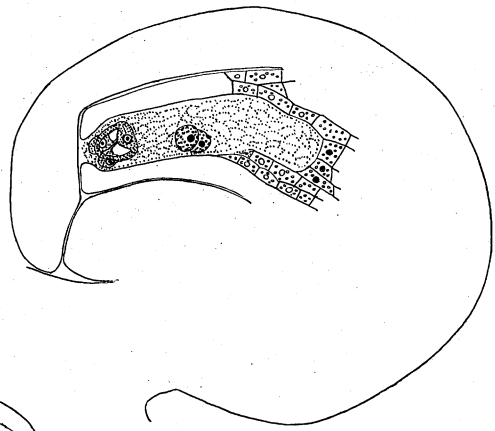
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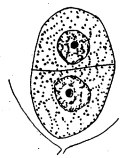
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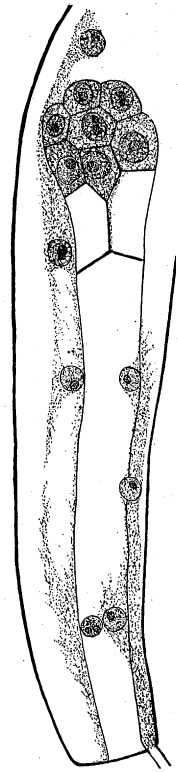
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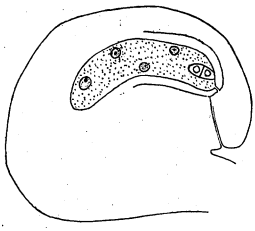
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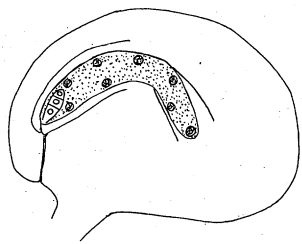
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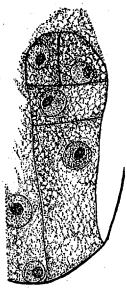
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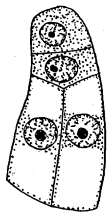
49

FIG. 36.—Embryo sac 8-nucleate, with large central vacuole and much starch; ×1500.

FIG. 37.—Vacuole in embryo sac has disappeared; polars in center of sac; sac is divided into three separate portions; only one antipodal cell; ×1500.

FIG. 38.—Mature embryo sac; polars in contact with egg apparatus; nucellus has disappeared at the micropylar end; ×360.

FIG. 39.—Proembryo with 4-celled suspensor; ×910.

FIG. 40.—Advanced stage of embryo; embryo has cut off epidermis; suspensor has thin cytoplasm and its cells are multinucleate; ×510.

FIG. 41.—Advanced embryo with suspensor showing on hypocotyl; ×360.

Vicia americana

FIG. 42.—Young nucellus with 5 archesporial cells; the integuments are appearing; ×1500.

FIG. 43.—Mother cell in synapsis; parietal cell has divided longitudinally; ×1200.

FIG. 44.—A row of 4 megaspores; ×750.

FIG. 45.—Functioning megaspore; much parietal tissue has developed; ×1500.

FIG. 46.—Mature embryo sac with nucellus eaten away; starch abundant in the inner integument and remaining portion of nucellus; polars on inner side of embryo sac and distant from egg apparatus; ×540.

FIG. 47.—The campylotropous ovule with mature embryo sac; ×330.

FIG. 48.—A 2-celled proembryo; ×1500.

FIG. 49.—A 4-celled proembryo; apical cell produces the embryo; ×900.

FIG. 50.—Proembryo in a view showing only one cell of each pair of cells composing the suspensor and the divided apical cell which produces the embryo; ×1200.

FIG. 51.—Suspensor distinct from embryo; basal cells of suspensor much elongated and multinucleate; the cells of the suspensor have very little cytoplasm; endosperm is parietally arranged; ×1200.

FIG. 52.—A 2-celled proembryo and 4 endosperm nuclei; ×360.

FIG. 53.—A 3-celled proembryo and 8 endosperm nuclei parietally placed; ×360.